LIFE-LONG AND TRANSGENERATIONAL EFFECTS OF EARLY EXPERIENCE IN ATLANTIC SALMON (*Salmo salar*)

By

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Abstract

Supportive-rearing programs to produce individuals for release in efforts to re-establish populations of threatened species continue to grow in number and scope. Based on the increasingly reported negative effects of captive exposure, we hypothesised that early captive exposure may affect fitness not only later in life but into the next generation, exactly when wild fitness must be present to contribute to sustainable population augmentation. We examined a supportive rearing program for endangered Atlantic Salmon (Salmo salar) that releases juvenile fish at two life stages (fry and parr) having varying duration of captive exposure. We followed multiple cohorts from release to the wild, collected 1-3 years later, held in a captive marine environment until maturity, and produced broods of offspring to examine effects of parental captive exposure on viability of the next generation. We found that the additional early-life captive exposure for parr resulted in smaller and younger smolts, adults, and smaller less viable offspring. Parr-origin fish survived better than fry from time of release until smolt stage as well as during captive marine rearing however, this is not likely indicative of improved wild fitness. We demonstrate how brief manipulations of early life exposure resulted in significant effects on fitness and present these findings in context of designing effective population recovery strategies.

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Co-Authorship Statement

C.N. Clarke, lead author and Master of Science in Environmental Science Candidate, was the major contributor to all portions of this work including conception, design, data collection, analyses, and writing. Secondary authors and academic supervisors, Dr. C.F. Purchase and Dr. D.J. Fraser contributed to each component as required and had significant and critical influence on project experimental design, data analyses and writing components. We intend to format and submit major portions of the work for publication in an appropriate scientific journal.

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Chapter 1.

General Introduction

Not surprisingly, an increasing number of populations threatened with extirpation around the world occur alongside increasing numbers of recovery programs aimed at augmenting them (Allendorf and Luikart 2007). Even though population crash timelines don't often permit strategy testing to indentify the best suited, recovery programs have been plagued with failure to reach population objectives (Beck et al. 1994). Considering the rate at which wild populations are identified as in danger of extirpation, resources to support recovery programs are unlikely to keep pace with the demand to implement them. As such, population recovery will increasingly depend on efficient execution of effective programs. To design effective recovery programs, managers require clear definitions of the recovery program outcomes that will be evaluated as program success and failure. Successful outcomes are increasingly found to be more complex than simply improving quantities of individuals. A growing area of study highlights the importance of measures of individual and population quality such as ability to reproduce (Fleming et al. 1997) and genetic variation (O'Reilly and Doyle 2007). Recovery programs which employ strategies to raise wild animals for part or all of their life in captivity to later release to the wild have been implemented for well over a century and described using a range of terms with varying degrees of similarity in definitions (i.e. enhancement, re-introductions, supportive rearing, stocking etc.). When similar strategies have different descriptions, comprehensive meta-analyses of strategy elements to determine which were associated with success/failure can be problematic. These issues contribute to the contemporary debate of which, or even if, recovery strategies should be implemented to achieve objectives of wild population maintenance or recovery (Snyder et al. 1996).

Across taxa, authors in the field of conservation biology continue to review and present collections of different species recovery strategies discussing which were successful and which were not in a variety of contexts (Price 1999; Fraser 2008). Despite programs often having simple objectives such as wild population augmentation, strategies to achieve objectives become difficult to link to results due to variability in species biology, individuals, populations, the environment and human induced effects on each. Further complicating simple correlation of program strategy with results is the growing body of literature on contemporary evolution providing insights into the rate at which evolutionary change can occur (Stockwell et al. 2003), observations of such 'rapid evolution' are no longer considered exceptions. As our understanding of the speed of evolution increases and the number of wild individuals to work with declines, the ability to benchmark recovery program status and link to initial objectives is further compromised.

Acknowledging that success and failure in augmenting wild populations results from many unknown and/or uncontrollable effects, recovery program managers should strive toward understanding the explanatory elements of why strategies failed or succeeded instead of which failed or succeeded. For example, where the recovery program objective is producing self-sustaining wild populations, individuals fit for wild survival and reproduction must necessarily be produced. In this example, program managers will benefit most from knowing what variables affect wild phenotype development for the species they are attempting to augment. This seems straight forward but represents a shift from the predominantly quantity-focused designs many recovery and augmentations programs have adopted for most of their history. Simply, if designers of population recovery programs understood what affected the development of wild phenotypes (any characteristics of physiology, morphology and behaviour), strategies could be

fashioned to promote it and thus maximize the probability of producing animals fit for wild survival.

This discussion is as relevant for fish population management as any other taxa. This is because programs to enhance wild fish populations for social, commercial, and ecological reasons date back over 150 years (Jonsson and Fleming 1993). Presumably, even with the most basic of record keeping, 150 years of enhancement practices, should allow straight forward statistical analyses to reveal explanatory elements in successful and failing strategies, however this is not the case and debate continues on recovery program design, why?

I propose that part of the explanation is in the inherent design of many of such recovery programs. With simple goals such as wild population augmentation, programs are often opportunistic and adaptive in executing strategies. This approach facilitates achieving short-term objectives sooner than would a rigid and more controlled approach but at the cost of experimental control for testing the effects of changing fixed variables (recovery strategies). For example, quantity of individuals released, life stage released, and release distribution, can and often does, change over time depending on program resources and support. Therefore, in well-resourced years, programs may have the ability to release several life stages instead of only one and/or distribute them wider in the environment. Any of these changes can cause results to vary when populations are subsequently monitored to determine strategy success. Although objectives of population augmentation could be reached in this example, it may be difficult or impossible to explain how each of the variations in program strategy contributed to the result and therefore difficult or impossible to replicate the results. That these fixed variables can change through time, while as many or more random variables (environment, survival, reproduction, etc) are

simultaneously affecting population outcomes, makes concluding trends in successful recovery program design difficult.

In the following thesis, by incorporating a long-term data set from a government program to recover endangered Atlantic salmon in Atlantic Canada with a short-term rigorous experimental design, we provide insight into explanatory elements of the results of two classic recovery strategies used for decades to enhance salmon populations across their range.

Our findings contribute to the knowledge base of principles of conservation biology above a standard assessment of strategy tradeoffs and would not have been possible to generate from "scratch" inside traditional graduate program timelines. To this end, and as suggested by Reed et al. (2010), we also encourage efforts in finding creative ways to incorporate similar long-term, large data sets with traditional experimental design toward producing more broadly applicable conclusions. As recovery programs to augment wild populations continue to increase in number and scope, their success depends directly on the ability of program managers to design and implement effective recovery strategies.

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Chapter 2

Introduction

Globally, it has been estimated that over the next two centuries, the number of species requiring some form of captive rearing support to avoid extinction will number in the thousands (Allendorf and Luikart 2007). Considering the social and economic importance of many species, it is obvious why recovery programs involving the captive rearing and release of wild-origin individuals are increasingly being adopted in efforts to lower extinction risk or re-establish self-sustaining populations. Many species of birds, mammals, and fish have been the subject of various forms of recovery program strategies around the world (Snyder et al. 1996)

A large proportion of recovery programs fail to meet population recovery goals due often to the negative effects captive exposure can have on populations through domestication selection (Price 1999; Fraser 2008). Domestication selection can cause genetic change by relaxing and/or re-directing selective pressures when selection for genotypes which are thriving in captivity occurs (Fleming 1994; Fraser 2008). Simply, domestication selection can allow more and different individuals to survive than natural selection would in the wild. In addition to these classic genetic effects of domestication (O'Reilly and Doyle 2007; Frankham 2008), it is now known that even short-term exposure of a wild individual to captivity, especially during early life, can induce plasticity in certain traits (de Mestral et al. 2013). Following re-introduction to the wild, these changes have been documented by many studies to compromise wild fitness (Price 1999; Von Cramon-Taubadel et al. 2005). Fewer studies address the effects of early environmental manipulation on the fitness of individuals much later in life or on the offspring they produce for the next generation. This should be of concern to recovery program managers because it is exactly at later stages and generations that the range of phenotypes available must

match wild environments when regeneration of self-sustaining populations is the recovery program objective. Following reviews on the effects of captive rearing strategies across taxa (Snyder et al. 1996; Fraser 2008), we hypothesised that the short- term demographic boost achieved by sheltering individuals from natural mortality early in life while in captivity would result in long-term or even trans-generational net-loss of fitness compared with strategies maximizing wild exposure early in life.

Atlantic and Pacific salmon populations have declined in many parts of their range, many receiving threatened or endangered status (Ford and Myers 2008; Chaput 2012). In response to these declines, considerable effort has been made to augment or re-establish populations using captive rearing recovery programs (Fraser 2008). Here, we examine a long-term (est. 2001) recovery program for Atlantic salmon from the Inner Bay of Fundy (IBoF) which releases juveniles of common genetic background at different life stages to the Upper Salmon River in Fundy National Park, New Brunswick, Canada. The fish studied here are either released to the wild just before first-feeding at the fry stage (fry-origin fish), or are fed in captivity for 5 additional months and released as parr (parr-origin fish).

We found that parr-origin individuals had higher survival rates than fry-origin from release to smolt stage and from smolt to adult stage in captive marine conditions. We discuss how the measures of fitness in which parr-origin were superior to fry are not likely indicative of natural fitness advantages but more likely a result of captive exposure effects and/or experiment limitations which prohibited the use of the natural environment during the marine phase for this salmon population. In illustrating that parr-origin fish had generally (but not exclusively) lower measures of natural fitness, we provide evidence for the prediction that early life exposure to captivity has life-long and trans-generational effects on fitness (sensu Frankham 2008; Fraser

2008; Araki et al. 2009), which might affect establishment of self-sustaining populations. We did this in 3 "Phases" (Figure 2.1) by following juveniles from release as fry or parr to viable eggs of the next generation.

The objective of many population recovery programs, including the one in Fundy National Park, is to augment numbers toward ultimately establishing self-sustaining populations in the wild. Where populations are not self-sustaining, programs must necessarily produce individuals fit for the wild environment using temporary captive rearing. Therefore, to design effective rearing strategies, understanding lifelong and/or trans-generational effects of varying amounts of captive exposure on fitness is important. We discuss potential mechanisms underlying the trends in observed effects and offer considerations in context of effective population recovery program design.

Methods

General

Population and recent recovery program history.

Fifty rivers draining to the Inner Bay of Fundy between New Brunswick (NB) and Nova Scotia (NS) Canada constitute the entire freshwater habitat for the unique and endangered Inner Bay of Fundy (IBoF) Atlantic salmon population (DFO 2010). Unknown factors limiting adult returns from the marine migration life-stage are considered the most important threats to population recovery (DFO 2010). As a result, the IBoF population's persistence currently depends on the Canadian Department of Fisheries and Oceans' (DFO) Live Gene Bank captive breeding recovery program (DFO 2008). The program's broad objective is to preserve and maintain IBoF genotypes and phenotypes. In NB, the program began with native wild founders

from Big Salmon River (BSR) and now artificially spawns and releases their decedents to the wild at various ages to later collect a portion of individuals for future broodstock.

Since 2001, Parks Canada has carried out IBoF salmon recovery efforts in Fundy National Park's (FNP) Point Wolfe River (PWR) and Upper Salmon River (USR) (Figure 2.2). Truly native salmon stocks do not likely exist for either the PWR or USR and both have been vacant for extended periods while both were blocked by logging dams near their mouths constructed at least as early as the 1930's (Hutchings 2003). Except for sporadic breaches, the PWR remained dammed until the mid 1980's. On the USR, regular access for salmon resumed during the early 1960's and returning adult salmon were observed by the hundreds and up to approximately 1000 during the late 1960s, all assumed to be strays from other nearby systems of the same IBoF population (Dadswell 1968; Hutchings 2003). A later genetic study confirmed this assumption (Fraser et al. 2007). Adult returns have been effectively absent since at least 2003 (FNP 2010 unpublished).

Current recovery efforts in FNP include participation in the ongoing DFO live gene-bank program currently maintaining the BSR. The BSR is located 50 km west of the park (Figure 2.2). Remnant wild smolts were collected from the USR in 2002-2003 and from the PWR in 2004 and 2005 for genetic identification. These were believed to be the last migrations of naturally occurring smolts as annual surveys suggested adult returns were effectively absent on the PWR and USR. Genetic analyses showed low levels of diversity in founder collections and BSR stock was used to supplement both river's broodstock populations to augment population genetic variation (O'Reilly 2004). The BSR stock was chosen to supplement the PWR and USR because it contained the nearest IBoF stock and because BSR stock had been periodically released to the vacant PWR in the past (Hutchings 2003). Releases of BSR-supplemented stock resumed on an

annual basis in 2003 on the PWR (adult salmon only) and 2006 on the USR (Age 0+ fry and parr only).

Study river.

USR is a rocky, steep gradient river with an average slope of 1.5% throughout the 9 km of accessible salmon habitat. Annual average discharge is 7.1m^3/s with a watershed area of approximately 175 km^2. Salmon-accessible river habitat is bound by natural water-fall barriers and the Bay of Fundy (Figure 2.2). Other native fish populations in the USR include American eel (Anguilla rostrata) and Brook trout (Salvelinus fontinalis).

Study sample origin.

Through 3 'Phases'(Figure 2.1), we observed effects of fry and parr release strategies by following selected cohorts from release stage through until eyed-egg stage of the next generation. Phase 1 observed two cohorts each of fry and parr as migrating smolts for effects on phenotype. With current survival in the wild between the smolt and mature adult stage on the USR being effectively zero the natural marine environment was unsuitable for our experimental goals of producing offspring once smolts matured. Phase 2 collected and reared 2010 smolts in outdoor marine net pens in the Bay of Fundy for approximately 16 months. Survival, growth, and estimates of maturity were recorded for Phase 2. We considered this environment to be a naturalized proxy for the first natural marine life stage at least when compared with indoor hatchery rearing in freshwater. Although naturalized, the captive marine environment still provided commercial feed and deliberate protection from predators. This is considered an experiment limitation which could have resulted in captive-suited individuals having superior measures of fitness during Phase 2 over individuals best suited for the wild. With current marine

survival rates in the lBoF, this was a necessary compromise to provide mature adults to examine in Phase 3. Phase 3 artificially spawned a subset of mature fry- and parr-origin fish to examine the effect of parental release-origin on offspring viability.

The smolts resulting from the release of 280,000 fry and 25,000 parr to the USR in 2008 and 158,000 fry and 29,000 parr in 2009 are the focus of Phase 1. Phases 2-3 (Figure 2.1) use the USR smolt collection of 2010 (n=1446).

The 2008 and 2009 releases originated from artificial spawning of broodstock which were collected as smolts from the BSR, PWR or USR from 2005 to 2007. O'Reilly et al. (2010) found 73-92 percent of juveniles produced from 2003 BSR-adult stocking to the PWR had one or two BSR parents and suggested other juveniles could descend from non-genotyped BSR parents or remnant residents which could include stray stocks from other sources such as the BSR or Petitcodiac River at the head of the Bay of Fundy. Broodstock collected from the USR could represent recently adapted stock (O'Reilly 2004) since the river became accessible in the 1960s but these fish contributed only 8 of 120 crosses released in 2009 (Table 2.1).

Because of the lack of native stocks and long-term vacancy of PWR and USR, the past releases of BSR stock to the vacant PWR, the recent releases of many families of BSR stock, and the close geographic proximity of the BSR to the study area, we are confident that our findings are not confounded by effects of family or local adaptations and are indeed the result of early exposure manipulation

Phase 1: Effects of early exposure on smolt phenotype.

Fry and parr were created from artificial spawning and indoor incubation in untreated ground water flow-through troughs at the DFO Mactaquac Biodiversity Facility in NB Canada (Figure 2.2). All fish were released over a section approximately 500 m long in the upper portion of the USR (Figure 2.2). Fry were released to the wild in spring before the onset of active feeding. Parr were randomly retained from mixed broods of fry and reared in tanks at the Mactaquac facility under more favorable conditions for growth compared to their counterparts in the wild. Notable rearing condition differences for parr included shelter from predation, daily consumption of commercial diet and elevated water temperatures compared to ambient river conditions. Parr were reared for 5 additional months after fry were released to the USR and then released in autumn of the same year. Exact numbers from each brood contributing to fry and parr releases are unknown because they mixed passively in captivity after hatching. Adipose fins were removed from all fish released as parr to distinguish them from fry-releases when collected later. Adipose fin clipping is widespread in fisheries management and is generally accepted (but see Reimchen and Temple 2004) to have no effect on behaviour or development (Vander Hagen et al. 2005).

The 2008 and 2009 releases were captured as migrating smolts from 2009-2012 using a rotary screw trap, a specialized live-trapping device for downstream-migrating salmonids (Flanagan et al. 2006). With effectively zero wild adult returns (FNP 2010 unpublished), all captured smolts resulted from past fry and parr releases. Trapping occurred from late April until mid-June each year beginning and ending with consecutive zero-catch days thus trapping was assumed to sample the entire migration. The trap was checked daily and smolts were collected for measurement onsite. FNP conducted a basic mark-recapture experiment and estimated that

capture efficiency for migrating smolt at that site was 10.5% in 2008 (FNP 2008 unpublished). This estimated efficiency is similar to longer running experiments on the nearby BSR using an identical trap to capture smolts that were released as fry and parr (Flanagan et al. 2006).

Fry and parr released to the USR migrated as one, two, or three-year old smolts. To track only releases of 2008 and 2009, ages were interpreted from scale samples taken from captured smolts for three years following both 2008 and 2009 releases (i.e. 2009-2012). In addition to age data, we recorded weights, migration date and fry or parr-release origin (presence or absence of adipose fin, respectively) for each captured smolt.

All statistical analyses were carried out using the Minitab16® software package (2012). Analyses of residuals, including evaluating assumptions of homogeneity, least squares, independence and normality were carried out. Tolerance of Type I error was set at 0.05.

A general linear model (GLM) routine was used to test for release stage effects on smolt age (A) with release stage (RS), release year (RY), and interaction term as independent variables. The interaction term of release year and release stage did not have a significant effect on smolt age and the term was removed. The model was described by ($A = \beta_o + \beta_{RS} RS + \beta_{RY} RY + \epsilon$).

A nested ANOVA (GLM routine) was carried out to determine whether migration day (Dm) depended on release stage (RS) controlling for release year (RY), age within a release year (A(RY)) and/or interactions between these factors. Nesting age within release year allowed us to compare migrating smolts of the same age from the same release year (and thus migration year) to determine if migration day depended on release stage. We found that smolts of the same age had insignificant differences in size regardless of release origin thus controlling for smolt age controls for size and adding a size term to this model would be redundant. Because of natural

variability in annual migration timing (early or late spring season etc.), comparisons of migration timing across migration years are not relevant to this question and so a nested model was appropriate to adopt. Interaction terms were insignificant and removed from the model. This model was described by $(\mathbf{Dm} = \beta_o + \beta_{RS}\,RS + \beta_{RY}\,\mathbf{RY} + \beta_{A(RY)}\mathbf{A(RY)} + \mathbf{\epsilon})$. Median migration day (MMD) is presented below and is described as the day of year at which 50% of the entire migration had occurred.

To test release stage effects on smolt weight, ANOVA tests in GLM routine were carried out with weight (W) as the dependent variable and release stage (RS), release year (RY) and interaction terms as independent variables. This model was described by $(W = \beta_o + \beta_{RS}\,RS + \beta_{RY}\,RY + \mathbf{\epsilon})$. The "RS*RY" interaction term was significant and this model was further broken down to determine the effect of release stage on smolt weight for each release year. The one-way model for each release year was described by $(W = \beta_o + \beta_{RS}\,RS + \mathbf{\epsilon})$.

Phase 2: Effects of early exposure on post-smolt growth, survival and maturation.

In May 2010, 1,446 smolts were captured from the USR, sampled as described above, and a single 2.5x12.5 mm 125htz passive integrated transponder (PIT) tag (BIOMARK inc.) was inserted in the dorsal musculature of each smolt on the day of capture for record tracking. All smolts were transferred by truck in oxygenated tanks to customized marine net pens operated by the aquaculture industry in the Bay of Fundy near the town of St. George, NB approximately 160 km west of FNP (Figure 2.2). Daily sorting of captures resulted in fry and parr-origin smolt being transferred in similar proportions, through the entire smolt migration, to each of 4 net pen rearing units (Table 2.2).

An array of four 3.6 m x 7.3 m x 1.8 m-deep rectangular marine net pens were divided at midpoints to yield eight 3.6 m^2 x 1.8 m-deep net pen blocks. All four pens were placed inside a 22 m (diameter) commercial sea-cage (Figure 2.3). Only one side of the array (4 blocks) contained fish at any time and fish were transferred by dip netting to alternate sides of the array during censuses of each block. This allowed nets to be removed, cleaned and inspected before the next census. Pen dividers were removed in April 2011 and fish were no longer reared in separate blocks. A standard census of each block was carried out six times at 1, 2, 3, 5, 14 and 16 months post-smolt. Standard censuses recorded only counts by release stage by noting adipose fin presence. Standard census counts were used to observe survival between release stages during marine rearing. Comprehensive censuses after 5 and 16 months, coinciding with the end of each summer growing season, collected lengths, weights, and tag identification in addition to count data. Periodic diver inspections of containment nets throughout Phase 2 found no breaches. Although sheltered and monitored daily, sources of mortality in net pens could include predation, parasite, stress, disease, or other causes but are assumed to affect both fry and parr in the same way. Because of unexpected PIT tag loss, only those fish retaining tags at comprehensive censuses are included in growth analyses of Phase 2. In the group which had lost tags by the end of Phase 2, the fry-origin:parr-origin ratio was similar to the group which retained their tags thus no tag retention by release stage bias is expected.

At the end of 16 months rearing, a final census was carried out and the first 100 fry- and 100 parr-origin fish netted, which retained a PIT tag, were held for Phase 3 and to allow estimation of maturity rates for each release stage. Remaining net pen fish were released to the Inner Bay of Fundy as part of a separate migration tracking experiment which was not part of our experiment.

Weight gain (Gw) was calculated by subtracting Phase 2 initial weight for each fish from Phase 2 final weight. Using an analysis of covariance (ANCOVA) in GLM routine, (Gw) was analyzed for Phase 2 with release stage (RS), entry weight (We) and interaction as independent variables. The interaction term of entry weight and release stage was insignificant and removed from the model. The model for weight gain was described as ($Gw = \beta_o + \beta_{RS} RS + \beta_{We} We + \epsilon$).

Survival (S) by release stage (RS) during Phase 2 was analyzed by calculation of the odds ratio of survival for fry to parr origin fish using counts collected during standard censuses from the first, third and fifth months of Phase 2 to the end of Phase 2. Significance of odds ratios was tested by binary logistic regression routine using a logit-link. To determine whether survival by release stage varied depending on time-period examined (i.e. survival from month 1 – end or from month 5 – end), we included a factor for census (Cn). This model was described as [$S_{Odds} = e^{(\beta o)} e^{(+\beta RS)} + e^{(+\beta Cn)} + \epsilon$]. The (Cn* RS) interaction term was significant, meaning that the survival odds ratio of fry to parr depended on census (time- period). The model was broken down post-hoc and survival of fry relative to parr was analyzed for 4 distinct periods of Phase 2; month 1-3, month 1-end, month 3-end, and month 5-end. These models (binomial error) were described as [$S_{Odds} = e^{(\beta o)} e^{(+\beta RS)} + \epsilon$] where $e^{(\beta o)}$=survival odds, for fry and $e^{(+\beta RS)}$=Odds ratio fry relative to parr-origin. These analyses used count data for each release stage (identified by adipose fin presence) from the noted census periods, not individual tag identifications. This allowed fish which had shed their tags to be included in the analyses but prohibited to the use of the 'Block' term as blocks were dissolved by removing dividing nets before the end of Phase 2 thus it was impossible to determine which block un-tagged fish originated from.

At the onset of spawning in late November, and using the retained group of 200 individuals, the odds of maturing (M) was calculated for each group. Significance of odds ratio of maturity was tested by binary logistic regression routine (binomial error) using a logit-link. This model was described by [$M_{Odds} = e^{(\beta o)} e^{(+\beta RS)} + €$]

Phase 3. Effects of early exposure on next-generation offspring viability.

As mentioned above, the first 100 fry and 100 par-origin fish carrying PIT tags at the final net pen census in September 2011 were transferred to a DFO hatchery in Mactaquac NB to carry out Phase 3 (Figure 2.1). In late November 2011, mature individuals were artificially spawned within treatment groups. The number of crosses completed was limited by maturation rate, available incubating space, and sex ratio of candidate parents. Twelve full-sibling pairs and two half-sibling pairs (14 females and 12 males with 2 males used twice) of fry-origin parents and nine full-sibling pairs of parr-origin (9 males, 9 females) parents produced broods of offspring. Individual broods were then held in separate containers in untreated ground water for two hours. After two hours, two replicates of 300 eggs each were extracted to incubation baskets labelled by cross and replicate. Following DFO Mactaquac fish culture protocols, all baskets of fertilized eggs were dipped in Ovidine™ disinfectant solution for ten minutes and placed haphazardly in a single, indoor, continuous flow, ground water incubation trough.

Prior to fertilization, each egg-lot was digitally photographed on 1 cm^2 graph paper background using a basic "pocket-sized" 12.0 megapixel digital camera. Using 1.47v imageJ (National Institutes of Health 2008) photo analyzing freeware scaled to the 1 cm^2 graph paper, we digitally enlarged each photo to the point where egg silhouettes began to blur and then measured the diameter across twelve random eggs from each female. Measurements for each

individual female were averaged to obtain mean egg-size per female. Fecundity was obtained (manually counted) from the same photos of each egg-lot.

Mean egg size (Se) by release stage, controlling for fecundity and female length was analyzed by GLM with release stage (RS), fecundity (F), female length (Lf) and interaction terms as independent variables. The interaction terms of fecundity and female length with release stage were insignificant and removed from this model. This model was described as: ($Se = \beta_o + \beta_{RS} RS + \beta_F F + \beta_{Lf} LF + \epsilon$).

Fecundity (F), controlling for female length, was analyzed by GLM with release stage (RS), female length (Lf) and interaction term as independent variables. The interaction term was insignificant and removed from the model. This model was described as: ($F = \beta_o + \beta_{RS} RS + \beta_{Lf} Lf + \epsilon$).

Opaque or otherwise damaged eggs were considered not viable and were removed and recorded weekly until after the "eyed-egg" stage 5 months following fertilization. Viable eggs for replicates of each cross were averaged and mean proportion viable eggs remaining at 5 months were recorded. Both replicates of one cross from parr-origin parents failed completely 4 weeks after spawning. This cross was considered an outlier and was conservatively removed from viability analyses.

To determine whether egg viability depended on parent release stage (RS) while controlling for female length(Lf), egg size(Se) and interactions, the odds ratio of egg viability for fry parents relative to parr was calculated using the average viability of replicates from each cross (i.e # viable eggs Replicate A+B/600). Replicates were averaged to avoid issues of pseudo-replicating female and egg size measurements which were collected only once for each cross.

Odds ratio was then tested by binary logistic regression. Interaction terms were insignificant and removed from the model. This binomial error model was described by [Odds= $e^{(\beta o)}e^{(+\beta RS)}$ + β_{Se} **Se** + β_{Lf} Lf + Є]

Results

Phase 1: Effects of early exposure on smolt phenotype.

An estimated 2%-3% of released fry and 13%-33% of released parr migrated as smolts (Table 2.3).

Parr-origin fish produced significantly younger smolts than fry-origin fish ($F_{1,2557}$=2192.4, p<0.001). Proportions of smolt ages for each release year consistently demonstrated that nearly 90% of fry-origin smolts migrate at age 2 while almost the same proportion of parr-origin smolts migrate at age 1 (Figure 2.4).

We found that fry and parr release strategies did not result in significant differences in migration timing when controlling for smolt age from the same release year ($F_{1,2543}$=2.14, p=0.144). Cumulative smolt migration (smolt run) timing for 2008 and 2009 releases are shown by age and treatment type in Figure 2.5.

The interaction of release stage and release year had a significant effect on smolt weight ($F_{1,2543}$=30.16, p<0.001). As a result, our model was simplified and a one-way ANOVA for each release year was carried out. These analyses showed that fry-origin smolts were significantly heavier than parr-origin smolts for both release years; 2008 releases ($F_{1,1185}$ =310.87,p<0.001) and 2009 releases ($F_{1,1357}$=821.96, p<0.001). These results show that the trend in smolt weight by release stages was consistent (fry larger than parr) but that smolts from 2008 and 2009 releases

were significantly different. Average weight of each group of smolts (release stage, release year, and smolt age) is shown in Figure 2.6.

Phase 2: Effects of early exposure on post-smolt growth, survival and maturation.

Although fry-origin fish had higher total weight gain in Phase 2, when controlling for initial weight begining net pen rearing, parr-origin fish gained more weight than fry-origin fish.

By the end of Phase 2, based on a sub-sample of 131 fry and 266 parr that had retained tags, release stage significantly affected weight gain when controlling for entry weight ($F_{1,396}$ =7.55 , p=0.006). Parr had a mean weight gain of 51.7grams/gram (g/g) of smolt entry weight (SD ±18.4 g, 95% C.I. 49.5-53.9) while fry gained 35.7 g/g (SD ±11.0 g, 95% C.I. 33.1-37.0,). Mean total weight gain was significantly different for each release stage (ANOVA, $F_{1,396}$ =56.45, p<0.001) and highest for fry at 1202.1g (SD ±327.6 g) compared to 969.7g (SD ±269.4 g) for parr.

In November 2011, maturity was determined on the subset of 200 individuals. Except for 12 mortalities (6 fry, 6 parr), 41/94 (44%) of parr-origin and 26/94 (34%) of fry-origin fish matured. Analyses showed odds ratio of fry:parr maturation was 0.67 (95% C.I. 0.37-1.20) and not significant (G=1.817, p=0.178).

Survival during Phase 2 was tracked using the counts of fry-origin and parr-origin post smolts collected from standard censuses which dip-netted and counted all fish from each net pen block (Figure 2.7a). Fry:parr ratios for all net pen blocks during the first summer show fry and parr were surviving similarly across rearing blocks (A,B,C,D) until blocks were dissolved (Figure 2.7b). The survival odds for fry-origin relative to parr-origin depended significantly on the interaction of release stage and census period analyzed (G=351.75, p<0.001), thus the model

was broken-down post-hoc. Simplified models showed fry-:parr-origin survival odds was 0.21 (95% C.I. 0.17-0.26) from month 1 to month 3 (G= 201.91, p<0.001). However, fry-origin relative to parr-origin survival was 1.45 (95% C.I. 1.04-2.01) from month 3 to the end of Phase 2 (G=4.99, p=0.027). Fry-origin relative to parr-origin survival was slightly better again from month 5 to end of Phase 2 at 1.51(95% C.I. 1.07-2.12) (G=5.68, p=0.019). Overall Phase 2 survival (month 1 – end) was 44% for parr-origin and 24% for fry-origin with a fry- to parr-origin survival odds ratio of 0.40 (95% C.I. 0.32-0.51) (G=63.58, p<0.001). Figures 2.7a and 2.7b show poor fry survival during the 3rd month and then fry survival remains stable while parr survival shows steady decline.

Phase 3. Effects of early exposure on next-generation offspring viability.

Fry-origin females produced significantly larger eggs than their parr counterparts when controlling for fecundity and female length (GLM, $F_{1,21}$ =21.34, p<0.001). Mean egg size for fry was 7.765 mm (SD±0.401) and 7.127 mm (SD±0.253) for parr. Female fecundity, controlling for female length was not significantly affected by release stage (GLM, $F_{1,21}$ =2.71, p=0.116). Mean fecundity for parr-origin females was 1980 (SD±487) and 1950 (SD±682) for fry origin parents.

Fry-origin parents produced significantly more viable offspring by 5 months following fertilization than parr-origin while controlling for egg size and female length. Odds ratio of fry- relative to parr-origin survival was 3.75 (G=334.97, p<0.001, C.I. 3.2-4.4). Mean proportion of viable offspring was 0.693 (SD±0.179) from the 14 broods of fry-origin parents ranging from 0.407-0.963. Proportion of mean viable offspring was 0.493 (SD±0.226) from 8 broods of parr-origin parents ranging from 0.030-0.780 (Figure 2.8).

Tables

2.1. Number of Atlantic salmon fry and parr released in 2008 and 2009 into the Upper Salmon River (USR) and rivers in which parents were collected from (Big Salmon River [BSR], Point Wolfe River [PWR], USR). Number of crosses contributing to each release group in parentheses. Fundy National Park, New Brunswick, Canada (Figure 2.2).

Release year & Stage	Parent collection river (# crosses)			Total Released
	BSR	PWR	USR	
2008 Fry	195000 (90)	85000 (52)	0	280000 (142)
2008 Parr	0	25000 (52)	0	25000 (52)
2009 Fry	35000 (42)	64000 (31)	58000 (8)	158000 (81)
2009 Parr	0	15000 (31)	14000 (8)	29000 (39)

2.2. Distribution summary of Atlantic salmon smolts captured from Upper Salmon River, Fundy National Park to marine net pen rearing blocks in Bay of Fundy. St. George, New Brunswick, Canada, 2010.

Pen Block	# Fry	% 2010 Capture	# Parr	% 2010 Capture
A	151	10%	172	12%
B	188	13%	197	14%
C	176	12%	197	14%
D	168	12%	197	14%

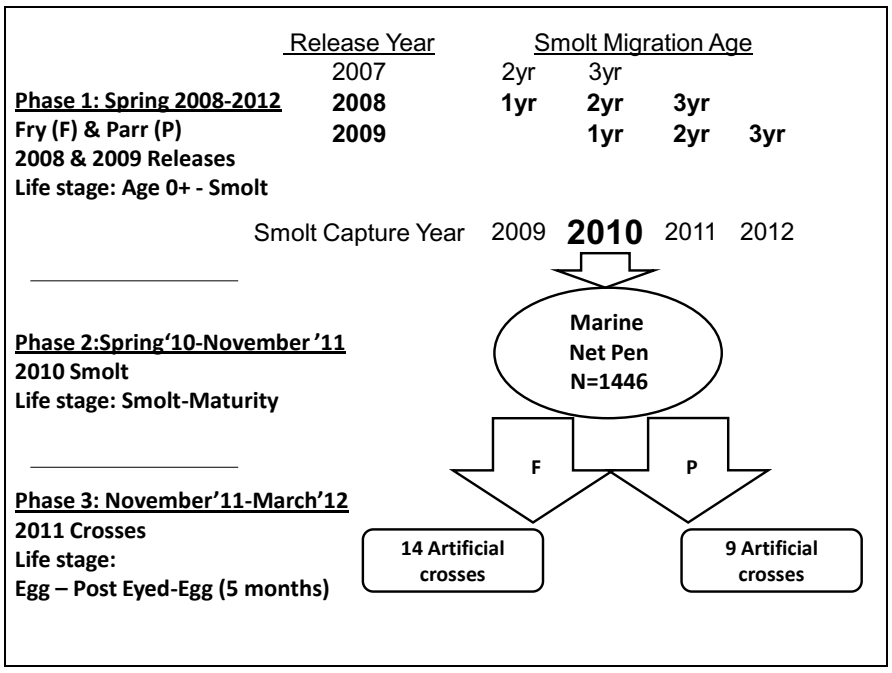
2.3. Estimates* of total Atlantic salmon smolt survival by age class from juvenile releases during 2008 and 2009 into the Upper Salmon River. Fundy National Park, New Brunswick, Canada. *Estimates based on 10.5% capture efficiency observed in 2008 USR trapping operations.

Release year & Stage	Released	Age 1	Age 2	Age 3	Total	Estimated Survival to Smolt Stage
2008 Fry	280000	779	6722	128	7629	3%
2008 Parr	25000	2751	624	0	3375	13%
2009 Fry	158000	284	2540	174	2999	2%
2009 Parr	29000	8152	1476	9	9638	33%

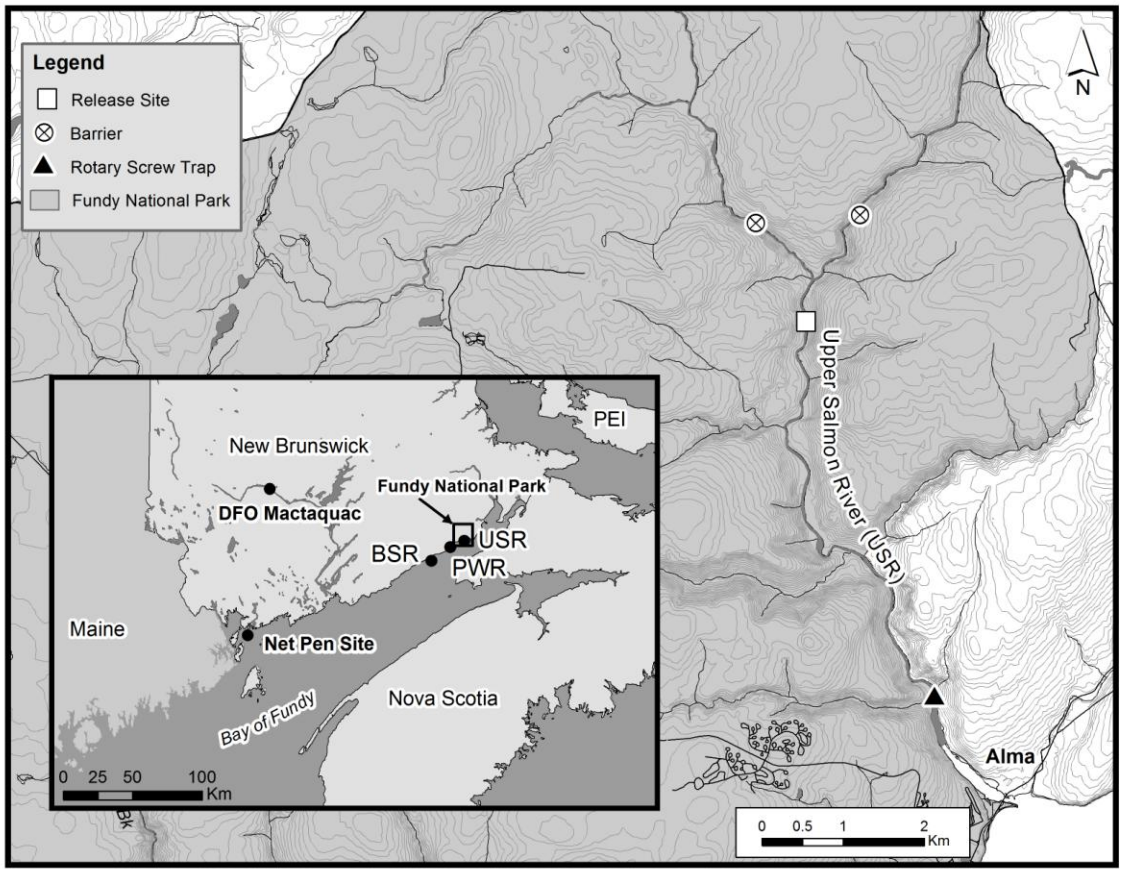
2.4. Summary of relative fitness measurements observed throughout Phases 1-3. Estimated fitness advantage column indicates which life stage demonstrated significantly higher levels of fitness for that measure. *Na indicates a measure in which differences between life stages was statistically insignificant using a 0.05 tolerance for type I error.

	Fitness measure	Fry	Parr	Estimated Fitness Advantage
Phase 1	Smolt age	Older	Younger	FRY
	Smolt weight	Heavier	Lighter	FRY
	Migration timing	Same	Same	na*
	Release-smolt survival	1-2%	13-33%	PARR
Phase 2	Rate of weight gain	Lower	Higher	PARR
	Final weight	Heavier	Lighter	FRY
	Maturation	Same	Same	na*
	Smolt-adult survival	24%	44%	PARR
Phase 3	Fecundity	Same	Same	na*
	Egg size	Larger	Smaller	FRY
	Egg viability	69%	49%	FRY

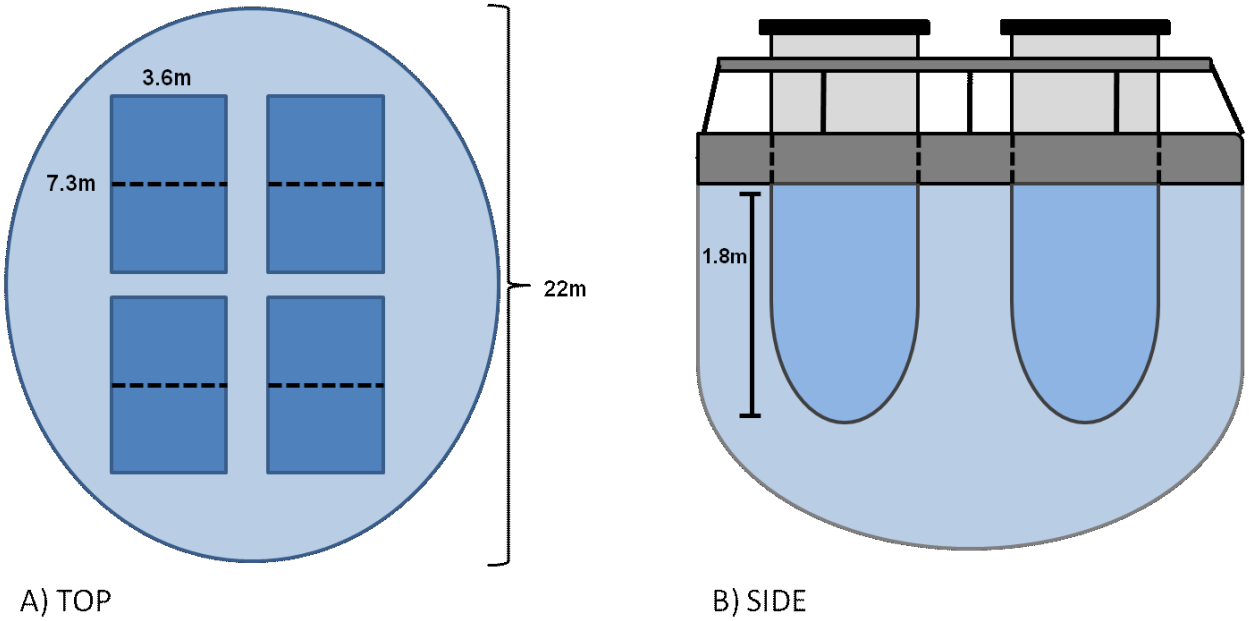
Figures



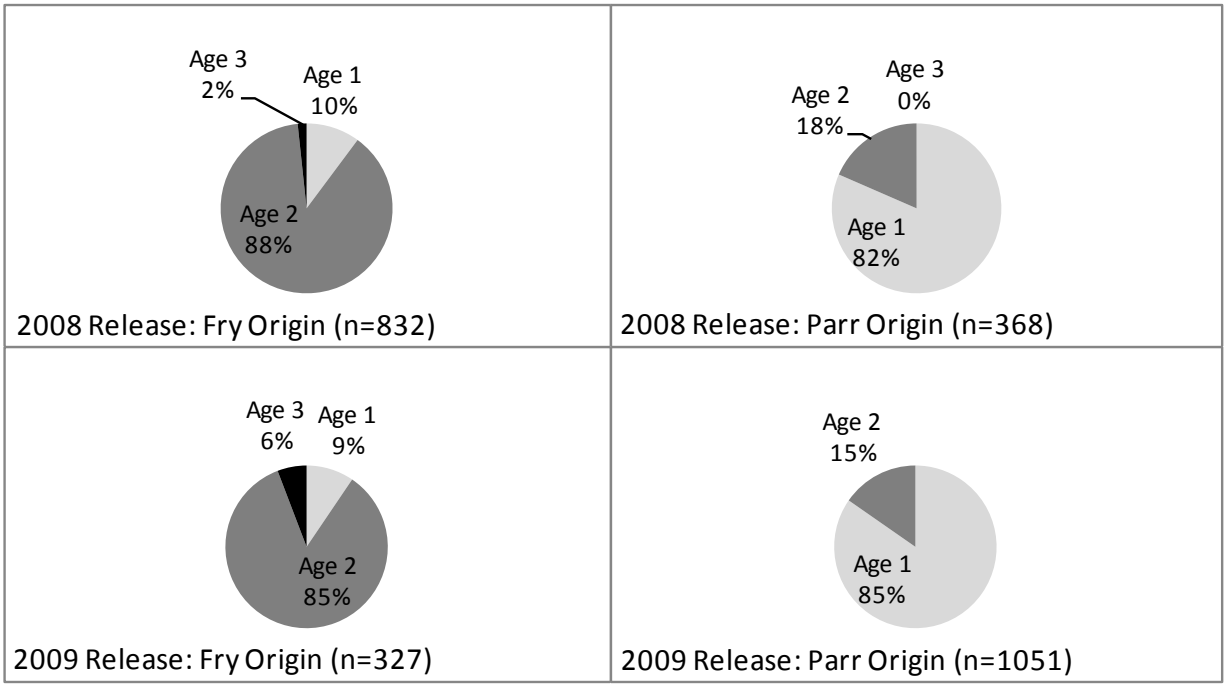
2.1. Flowchart outlining project phases across salmon life stages. Phase 1: 2008 and 2009 fry and parr releases captured as migrating smolts in spring of 2009 - 2012. Phase 2: 2010 smolts captured and reared in marine net pens May 2010 – September 2011 with subset retained at hatchery until November 2011. Phase 3: Offspring created from fry- and parr-origin parents monitored for 5 months November 2011-March 2012.



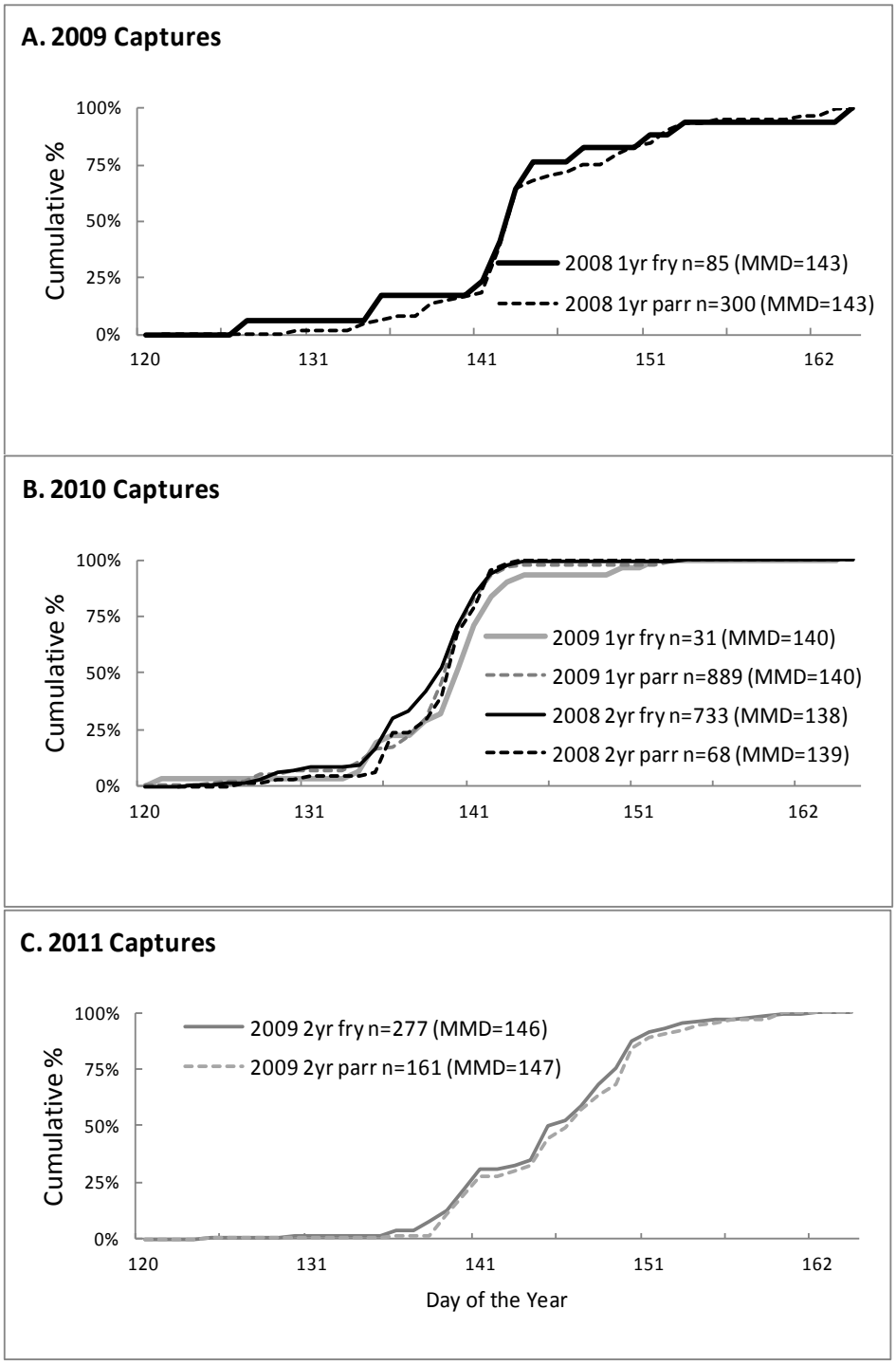
2.2. Map of study area in context of Eastern Canada. Upper Salmon River (USR) and Point Wolfe River (PWR) in Fundy National Park. Big Salmon River (BSR) and the Department of Fisheries and Oceans (DFO) Mactaquac Biodiversity Facility, New Brunswick, Canada.



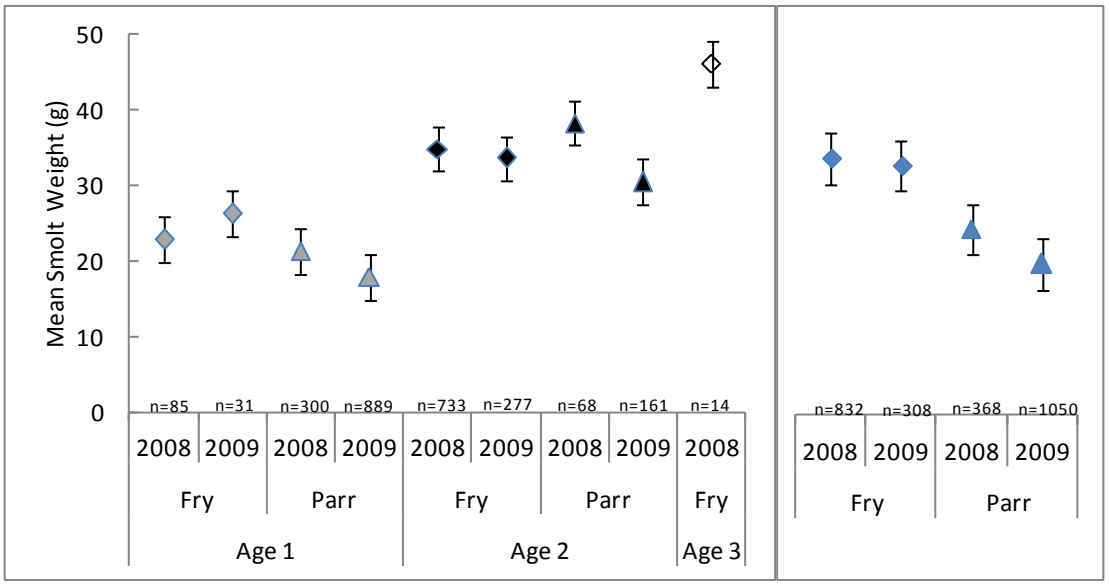
2.3. Top (A) and side view (B) diagram of net pen block array. Inside a standard 22 m diameter commercial sea cage, four customized 7.3 m x 3.6 m x 1.8 m-deep experimental pens were divided by netting (dotted line in Top view) to yield 8 total blocks. Only two pens (4 blocks) contained post-smolts at any time to allow for net inspection and cleaning between each census to monitor survival and growth. Dividers were removed in April 2011. St. George, New Brunswick, Canada



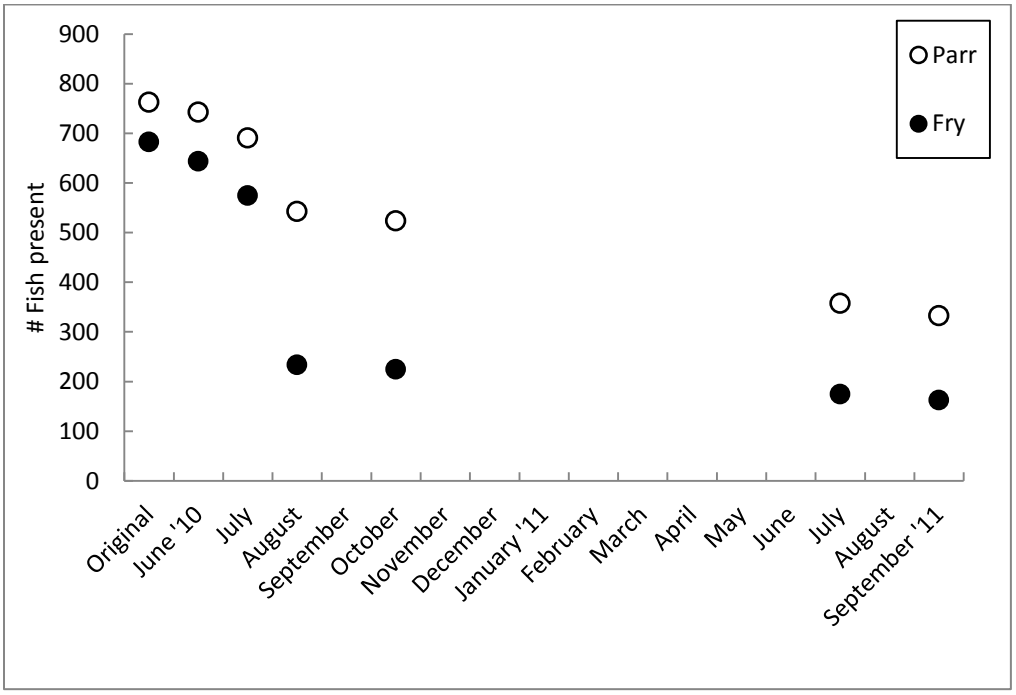
2.4. Smolt age proportions by release stage from 2008 and 2009 fry and parr releases on Upper Salmon River, Fundy National Park, New Brunswick, Canada.



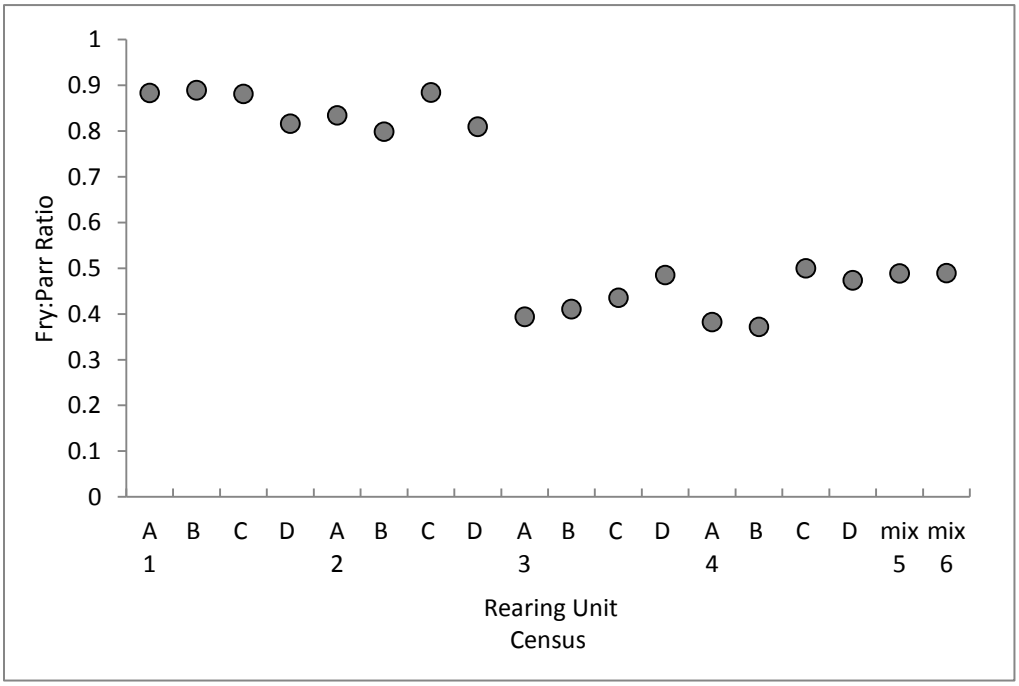
2.5. Cumulative proportions of smolts migrating from 2008 and 2009 releases. Median Migration Day (MMD) shown in parenthesis, is defined as the day of the year in which 50% of the total cohort had migrated. Upper Salmon River, Fundy National Park, New Brunswick, Canada.



2.6. Summary of outmigtating Atlantic salmon smolt weights. Left panel: Summary of mean ± SE smolt sizes by age (symbol color), release stage (symbol shape), release year. Right panel: overall mean by release stage and year. Upper Salmon River, Fundy National Park, New Brunswick, Canada.

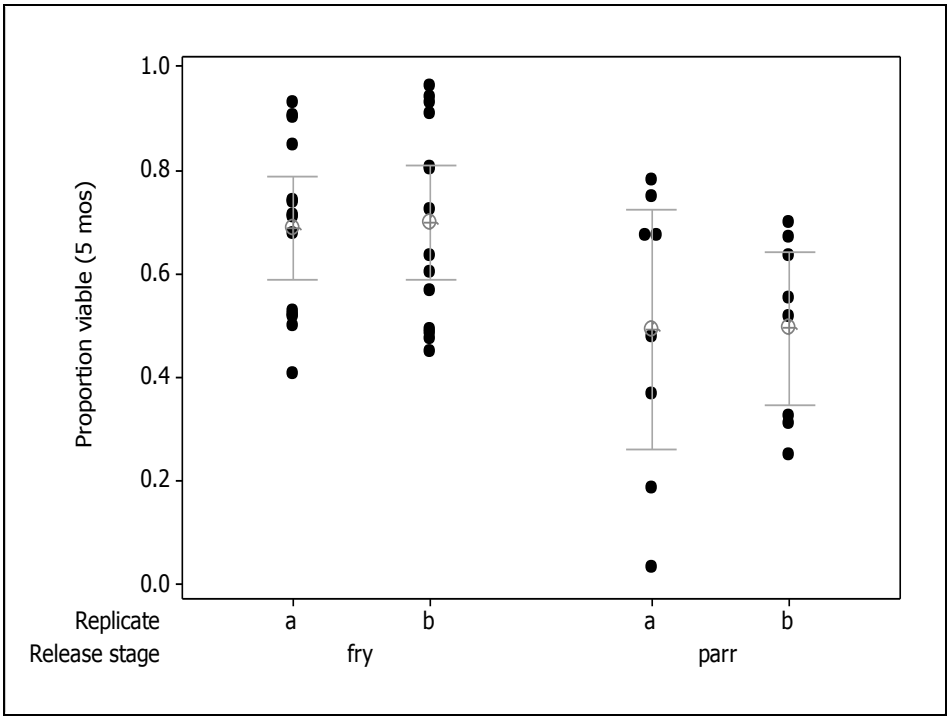


A



B

2.7. A. Total counts by release stage during standard censuses conducted in June 2010(1), July 2010(2), August 2010 (3), October 2010 (4) July 2011 (5) and September 2011 (6). B. Ratio of Fry-origin:Parr-origin post smolts (Fry Count÷Parr Count) counted at each census for each net pen block*.*All Blocks combined for 5th and 6th census.



2.8. Proportion viable eggs produced from marine pen-reared 2010 Upper Salmon River smolts remaining after 5 months incubation by parent release stage and replicate group. Measurements (closed circles), mean (open circles) and 95% confidence interval bars shown.

Discussion

By tracking two cohorts of salmon from release as age 0+ juveniles through to viable offspring of the next generation, this study found repeated evidence that varying early life exposure induced divergence in several phenotypic traits throughout life and into the next generation which are known to be important for lifetime fitness (Table 2.4). Specifically, we found that juvenile salmon released into the wild as unfed fry produced fewer but older and larger smolts, fewer but larger adults after rearing in a captive marine environment, and larger and more viable offspring, when compared with parr-release origin fish that were captive reared during the first 5 months of external feeding. In context of other studies, we offer explanations for the apparent improved survival of parr-origin fish during Phase 1 and 2 and conclude that overall, the increased duration of early-life exposure to the wild for fry-origin fish contributes to improved levels of wild fitness.

Phase 1: Effects of early exposure on smolt phenotype.

Our results show that smolts which were released at the parr stage migrated predominantly at age 1, while smolts released as fry migrated a year later. Parr-origin fish spent the first 5 months of external feeding (post-yolk sac) in more favorable growing conditions than their fry-counterparts experienced in the wild. It has been shown that growth rate and size attained by the fall prior to smolt migration determines whether or not 'smolting' will occur (Elson 1957; Okland et al. 1993). Further, faster growing juveniles tend to migrate as younger, smaller smolts whereas slower growing juveniles migrate at older ages and larger sizes (Jonsson 1985). Attributed mainly to improved growing conditions during their extended captive

experience, the tendency of age 0+ parr releases to migrate as younger smolts has been previously observed in this and other populations of salmon (Skilbrei et al. 2010; de Mestral et al. 2013). In our study, the effect of varying early exposure on smolt age resulted in most parr-origin smolts having 17 months less time in the wild than fry-origin smolts. Although our study system did not permit the estimation of smolt to adult survival in the wild, decreased exposure to the wild during early life stages has been shown to have negative effects on lifetime fitness for wild-origin individuals when returned to nature in other salmonid populations (Jonsson et al. 2003; Vollestad et al. 2004).

Contrary to expectation, variation in early life exposure did not significantly affect seasonal migration timing when comparing smolt of the same age from the same release cohort. In the nearby BSR, de Mestral et al. (2013) found variable results in migration timing when observing smolts produced from either wild returns, fry releases, or parr releases. Specifically, they found fry-origin smolts migrated at the same time as one generation of parr-origin smolts but significantly later than wild- and a second generation of parr-origin smolts. Kennedy et al. (2012) found Atlantic salmon smolts with previous captive exposure migrated earlier than wild counterparts on the River Bush in Ireland. Hoar (1976) showed that older Atlantic salmon smolts are generally larger than younger smolts in the same system and run earlier in the migration with better ability to escape predation and tolerate salinity. In other systems, stocked age 0+ parr migrated later, younger and at smaller sizes than those stocked at earlier stages partly because of size being positively related to salinity tolerance (Saltveit 2006; Skilbrei et al. 2010). Here, even when comparing fry- and parr origin smolts of different ages and release years in the 2010 migration, median migration day for each cohort varied only by two days. The USR is a relatively small river system with only 9 km of accessible habitat and juveniles are all released to

the same upper reaches. Less habitat area would lower the opportunity for smolts of different ages/sizes to distribute independently and possibly contribute to observed insignificant differences in run timing in our case. Further, other studies have shown salmonid migration timing to be a population-specific trait (Kallio-Nyberg and Ikonen 1992; Pascual and Quinn 1994) and we examined predominantly one stock from a single population which may explain a lack of differential migration timing.

Due to older age at migration, fry releases produced larger smolts than their parr counterparts. Although release stage significantly affected smolt size, there was no difference in sizes of smolts of the same age regardless of release stage. This suggests that early exposure did not directly affect smolt size but rather smolt age, and because of the significant effect release stage has on smolt age, sizes were affected accordingly. It is documented in other salmon populations that larger smolt size is related to higher marine survival which would increase reproductive success in anadromous salmon (Farmer 1992; Lundqvist et al. 1994; Antonsson et al. 2010). Further, Jones et al. (2013) recently showed BSR smolts of fry-release origin had twice the adult return rate of parr-release origin smolts but still only about a fifth the return rate of wild smolts. Lacroix and Knox (2005) also found smolt size and age are positively related to salmon survival in the Bay of Fundy. This suggests expected decreased marine survival for parr-origin smolt entering natural marine conditions despite what observed improved survival during Phase 2 of our experiment.

As expected, variable captive exposure times which lead to most fry-origin smolts having 17 months more wild exposure than parr-origin counterparts resulted in different smolt escapement rates. From releases in 2008 and 2009, an estimated 2-3% of fry and 13-33% of parr,

respectively, survived from release to migrate as smolts. Survival to a future life stage is understandably a common metric in population recovery programs to measure strategy efficacy because captive rearing time is positively related to costs and negatively related to quantity of released individuals (Jonsson et al. 2003; Jonsson and Jonsson 2011). When multiple release strategies are employed, survival to a future stage is often used in strategy comparisons (Bilton et al. 1982; Farmer 1992). Comparisons of survival are misleading when measured from or to different life stages. Further, if the release strategy directly affects the time between stages (as in this case with smolt ages), comparisons become even more ambiguous. For wild Atlantic salmon, the life stages of significant diet change, such as at hatch and smolt are known as periods of relatively high inter-stage mortality (Cunjak and Therrien 1998; Jonsson and Jonsson 2011). Here, parr-origin fish were fed and sheltered in captivity after hatching, released 5 months later and most migrated as smolt after only 7 months of wild residence. Conversely, for most smolts of fry-origin, wild residence and associated exposure to wild selection pressure is nearly 24 months long. It is unclear in our study whether fry and parr of the same age were surviving differently in the wild as we tracked only from release stage to smolt stage. Comparison of survival to smolt for each strategy, if made at all, should be with a clear understanding of this situation.

Managers assessing recovery strategy tradeoffs should consider that some strategies could produce demographic boosts at the next life stage (i.e. parr-origin produced proportionally more smolts than fry-origin releases) but fail to achieve population level objectives. Instead, programs should strive for designs yielding the most individuals best fit for lifetime wild survival and reproduction of viable offspring when establishing self sustaining-populations is the objective.

Phase 2: Effects of early exposure on post-smolt growth, survival and maturation.

Despite entering the captive marine environment of Phase 2 as significantly smaller and younger smolts, parr-origin fish gained more weight relative to initial weight, matured similarly, and survived better during Phase 2 than fry-origin smolts exposed to identical conditions. However, fry-origin smolts gained more total weight during Phase 2. Interestingly, and similar to findings by Dempson et al. (1999), fry had extremely high mortality during the first 3 months of captive marine rearing which resulted in parr-origin fish having higher overall Phase 2 survival.

That parr-origin grew at a faster rate in the marine net pens could be attributed to their younger age and/or the fact that parr-origin fish had previous experience with feeding in captivity during early life whereas fry-origin smolts do not. Early life stages for salmon are known to be important for learning and behavioural development (Khislingher and Nevitt 2006; Salvanes et al. 2013) as well as high cumulative mortality (Cunjak and Therrien 1998). This suggests that even parr released to the wild for a period of time would be better adapted to, living in captivity later in life (including consuming commercial feed) than their fry-origin counterparts with no captive feeding experience. However, fry-origin fish gained more total mass and were larger fish at the end of the post-smolt life stage.

Fry-origin fish began Phase 2 in a 0.88:1 ratio with parr-origin fish but were 0.49:1 by the end (Figure 2.7). Using only beginning counts of fry- and parr-origin fish for Phase 2 and counts collected at the end of Phase 2, we found that 44% of parr-origin fish survived marine rearing while only 24% fry-origin survived (Table 2.4). This was due mostly to the very poor survival of fry-origin fish within the first 3 months. After 3 months, fry-:parr-origin survival was stable and

favoring fry-origin fish for the remainder of Phase 2. Our observed increase in fry mortality during July is similar to July peaks in mortality in wild Atlantic salmon smolts reared in marine pens in Newfoundland, Canada by Dempson et al. (1999). In that study, failed smolt syndrome (McCarthy et al., 1996) was attributed to the increased mortality as wild fish did not recognize or adjust to commercial feed. Considering our fry-origin smolt also had no experience consuming commercial feed, it is reasonable to suspect failed smolt syndrome contributed to our observed increase in fry-origin smolt mortality. The overall increased survival of parr-origin fish during Phase 2 illustrates a limitation of our experiment. Because the natural marine environment could not be used to determine differential survival for fry- and parr- origin smolts, a captive marine environment was the most feasible means to meet our experiment objectives for Phase 3. By tracking survival at many points in time during Phase 2, we show that after initial higher mortality of the fry-origin group, they survived better than parr-origin post smolts. This supports the assertion that superior Phase 2 survival for parr-origin fish is likely an effect of rearing in a captive environment which is more familiar to them and not necessarily indicative of improved wild fitness.

Maturity status was determined on a subset of 94 fry and 94 parr-origin adults during their spawning period. From the subset, we found that observed differences in maturation of fry and parr-origin fish were insignificant despite the observed proportion of mature parr-origin fish being slightly higher than those originally released as parr. Maturation age has been negatively related to growth rate in other salmon populations (Jonsson and Jonsson 2011). Here, due to improved early growth conditions and familiar post-smolt rearing conditions, the predominantly younger parr-origin smolts grew at a faster rate and matured at the same rate as the older fry-

origin smolts which follows long presented findings that faster early growth rates result in earlier maturity in salmonids (Alm 1959).

Phase 3. Effects of early exposure on next-generation offspring viability.

We have provided evidence of trans-generational effects of early life exposure as fry-origin parents produced significantly larger and more viable eggs than parr-origin parents. Jonsson et al. (1996) showed that growth rate during early life was negatively related to egg size evidenced by hatchery reared smolts growing faster but having smaller eggs after maturing in the wild than counterparts which reared entirely in the wild. In that study, producing larger eggs was suggested to be a response to wild fish experiencing less favourable growing conditions early in life. Similarly in our work, parr had higher growth rates than fry in both pre-, and post-smolt life stages and produced smaller and less viable eggs. Larger eggs produce larger fish after the onset of feeding, which is related to higher survival and a competitive advantage over smaller fish (Einum and Fleming 2000; Burton et al. 2013). This suggests a survival advantage for offspring of fry-origin fish released to the wild as a part of efforts to establish self-sustaining populations.

Conclusions

Except for the first 5 months of active feeding, Atlantic salmon observed here were exposed to the same conditions from fertilization to maturity, but exhibited significantly different phenotypes throughout life and into the next generation. Table 2.4 summarizes key measures of fitness observed in this study. We conclude that the increased wild exposure of fry-origin fish resulted in important fitness advantages throughout life and into the next generation. However, parr-origin fish demonstrated improved levels of fitness by having higher survival than fry-origin counterparts from release to smolt and during Phase 2 captive marine rearing. We assert these results are not reflective of improved wild fitness levels for parr origin fish. As explained above, comparing release stage to smolt stage survival can be misleading becuase of the effect release stage had on duration of wild residence. Further, there are repeated findings of IBoF Atlantic salmon smolt survival at sea being positively related to smolt size, age, and length of wild exposure (Lacroix and Knox 2005; Jones et al. 2013). Thus, the improved survival of parr-origin fish during Phase 2 is likely due to their familiarity with captive rearing instead of improved fitness and based on other IBoF salmon studies, we would expect the older, larger, and more wild-experienced fry-origin smolts to have better ability to survive the natural marine environment.

Selective pressures are strong for species that have high cumulative brood mortality (i.e. egg stage to spawning stage) such as salmon. For managers of supportive rearing programs to recover such populations, the implication is that even brief (relative to lifetime) deviations in early exposure can produce lifelong and transgenerational effects on important measures of fitness.

Because significant cognitive development (Kihslinger and Nevitt 2006; Chittenden et al. 2010; Salvanes et al. 2013) and highest cumulative mortality (Cunjak and Therrien 1998) occurs from egg-smolt stages in Atlantic salmon, these earliest life stages most shape the raw material available to produce the next generation. Accordingly, managers should prefer wild environments shaping a population at these most plastic stages when the objective is to produce self-sustaining populations which are fit for the wild. Program managers should consider the relative plasticity of various life-stages for the species they are attempting to recover and strive to at least naturalize if not totally avoid captive rearing during the most plastic stages or stages which experience intense selective pressures resulting from high rates of mortality and/or development.

In the case of the IBoF salmon population, considering the magnitude of effects observed by manipulating early life stages and the ongoing hypothesis that it is marine life stages and not the earlier freshwater life stages that are most limiting population recovery, minimal, if any, manipulation of freshwater life stages (spawning-smolt stage) should be planned. With available evidence, we suggest that the ideal IBoF recovery program would intervene only during marine life stages. For example, intercept individuals just prior to or during the marine phase (near the smolt stage) and return them at the adult stage just prior to or during their natural re-entry to freshwater phases. This way, only the currently limiting life stages are artificially manipulated and the stages of most intense selection and development occur in the wild, free from the proven effects of domestication. In less-ideal scenarios where captive spawning is required, earliest possible life stages (i.e. egg>fry>parr>smolt etc.) should be released to the wild to maximize wild experience during earliest life stages and increase the probability of producing individuals which are more shaped by, and therefore more fit for, life in the wild.

Recent findings by de Mestral and Herbinger (2013) showed anti-predator response in IBoF salmon was negatively related to generations in captivity. This follows our recommendations to allow natural elements to shape populations when natural fitness is the objective. Complimentary research to de Mestral and Herbinger (2013) to determine whether measures of fitness are positively related to generations spent in the wild would help confirm validity of our recommendations and provide valuable knowledge designing effective recovery strategies.

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Chapter 3

General Conclusion

By incorporating data from a long-term recovery program using two classic strategies for augmenting wild salmon populations with a rigorous short-term experiment, we demonstrated brief alterations in early life exposure had life-long and transgenerational effects on measures of wild fitness.

Our design isolated the source of observed effects on fitness throughout life and into the next generation to brief differences in environmental exposure early in life. This allows one to consider the mechanisms at play early in life which are cued by environmental exposure to result in the effects on fitness observed in our study. With increasing use of recovery programs by jurisdictions with varying amounts of support and resources, understanding what drives observed trends in fitness reduction resulting from captive exposure is important for developing effective strategies with available resources. Findings of improved measures of natural fitness with increased wild exposure early in life are well established for Atlantic salmon (Jonsson and Jonsson 2011). Mortality from egg stage to smolt stage is also well studied in Atlantic salmon populations and egg-smolt survivals vary within and between populations but commonly range from <1%-3% (Cunjak and Therrien 1998; Jones et al. 2010; Kennedy et al. 2012). Although studies of survival from one stage to the next are well common for several populations, fewer report lifetime inter-stage survival of entire salmon generations to allow reporting of cumulative rates of mortality. From studies that do follow inter-stage survival for cohorts across many or all life stages, it is clear that cumulative mortality rates for salmon are at or near peak rates during earliest stages. In wild populations, Cunjack and Therrien (1998) estimated approximately 70%

mortality from egg to 0+ (years old) fry stage while Kennedy at al. (2012). estimated 92%. These studies estimate that the cumulative mortality rate is highest during the earliest stages, decreasing in later stages until approximately 97%-99% cumulative mortality (from egg) is reached by smolt stage. A more recent and growing field of study in salmonids is showing that significant cognitive development also occurs very early in life for this animal (Kihslinger and Nevitt 2006; Chittenden et al. 2010; Salvanes et al. 2013). For example, Kihslinger and Nevitt (2006) showed critical regions of 3 week-old salmonid brains develop least in plain captive environments, more in complex naturalized captive environments, and most in wild environments. Interestingly, these findings parallel measures of wild fitness observed in other salmon populations such as survival during the marine phase where Jones et al. (2013) found smolts with least wild exposure as juveniles had lowest marine survival and smolts with most wild exposure had the highest.

Certainly, knowledge gaps remain to understand lifetime rates of mortality and development in salmonid populations although current literature suggests that rates of both are high, if not maximal, early in life and likely decreasing with age. If this is indeed the case, the earliest life stages for this animal may most affect which individuals are available for the next life stage. In a contrasting hypothetical example, life stages undergoing no mortality or development (cognitive or otherwise) change the population very little, if at all, for the next life stage. If the theory of high and decreasing rates of mortality and development earliest in life are accurate, it becomes clearer why even briefly exposing the earliest stages to captivity significantly compromises wild fitness later in life and why increasing earlier wild exposure augments wild fitness later in life. In our study, increased early exposure to the wild for fry-origin fish improved measures of wild fitness later in life such as smolt size, smolt age, size at maturity and offspring viability. In contrast, increased captive exposure for parr-origin fish

induced divergence from wild phenotypes (producing younger and smaller smolts) but interestingly, their increased early captive exposure likely contributed to their improved survival over fry-origin fish in the captive marine environment experienced later in life. That early life exposure shapes lifelong fitness measures is increasingly demonstrated for several species (Price 1999). Of particular importance to species recovery programs aimed at producing self-sustaining wild populations through the release of captive exposed individuals, transgenerational effects of early life captive exposure are increasingly being reported as we have demonstrated here and as demonstrated in other salmon populations (Fleming et al. 1997; Araki et al. 2009) and other fish species (Taborsky 2006).

For the Inner Bay of Fundy Atlantic Salmon population observed in this study, we found brief increases (relative to life-span) in captive exposure during early life stages, compromised critical measures of wild fitness for this animal such as smolt size, size at maturity and offspring viability and interestingly, may have increased measures "captive-fitness" when parr-origin fish thrived when re-introduced to captivity later in life. In context of effects of manipulating early life exposure, our findings are broadly applicable to designers of recovery programs considering strategy tradeoffs. For example, with the recovery objectives of establishing self-sustaining wild populations, if the only strategies available were fry and parr releases, we showed that fry, with less captive exposure, will likely exhibit higher levels of wild fitness throughout life and into the next generation. However, with the knowledge of wild fitness being negatively related to early life captive exposure, other managers could design improved strategies which further reduce captive exposure early in life such as releasing fertilized eggs or, if their resources permitted, releasing adults (ideally with maximal previous wild exposure) to spawn naturally and produce juveniles totally free of captive experience. On the other hand, if resources permitted only release

of smolt or parr stages, our findings would suggest parr would likely exhibit the least compromises to wild fitness because of greater wild exposure early in life.

Our recommendations to managers of recovery programs that endeavor to maintain or establish wild populations are therefore to consider maximising early exposure to the wild with the resources they have at hand rather than suggesting any particular strategy.

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